RELATION BETWEEN TOP AND ROOT SIZE IN HERBACEOUS PLANTS*

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In his Treatise on the Physiology of Plants SORAUER affirms that the plant must not be looked upon as an unchangeable organism, restricted to a definite form, but as being plastic, capable of further modification in any of its parts; its usual shape being susceptible to alteration, within certain limits, as if it were made of wax. This principle has been substantiated by the practical gardener, who, besides seeking to grow herbaceous plants in situations to which they are the best adapted by nature, often endeavors to cultivate them successfully in special localities, and, in all localities, seeks to render them more useful to his purposes.

Perhaps chief among the attempts of the gardener at altering normal physiological functions and interfering with the ordinary course of development is that of remodelling certain plants with respect to the relative size of top and root. His success in this effort has been remarkable; so much so that there might seem to be an attainable "ideal balance" between size of top and root for every particular desire or necessity. However, the limits mentioned by SORAUER must exist, making it impossible to proceed beyond a certain point with a given species, and also rendering it likely that even within the limits set by nature, increasing or decreasing the normal development of either top or root in order to favor the other part may result in danger to the plant as a whole except this be attempted by persons who thoroughly understand the plant and its conditions of life and vigor. Obviously, the aerial and subterranean portions of a higher land plant are mutually dependent, since the roots furnish the raw nutrients and water obtained from the soil and often serve as places of storage, while the tops supply the elaborated organic compounds essential for growth. It is of practical significance and also of considerable scientific interest to determine the nature of this relationship, or, more specifically, to determine how much variation in this state of reciprocity occurs naturally, and how much may be induced experimentally.

Literature

Interest in the proportionate size of the top and root of the plant is of long standing. The following quotation is from the ancient writings of VARRO (7): "In autumn and winter the roots develop more than does the leaf of the plant because they are nourished by the warmth of the roof of

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earth, while the leaf above is cut down by the frosty air. We can learn this by observation of the wild vegetation which grows without the intervention of man, for the roots grow more rapidly than that which springs from them, but only so far as they are actuated by the rays of the sun. There are two causes of the growth of roots, the vitality of the root itself by which nature drives it forward and the quality of the soil which yields a passage more easily in some conditions than in others."

These early observations have been followed in more recent times by numerous experimental studies on the relation of top and root size, use having been made of many different species and varieties of herbaceous plants. A chronological review of the literature shows by way of generalization that there has been an increasing tendency to seek the causes underlying variations in relative growth of top and root, and also to subject the data obtained to more complete mathematical analysis and interpretation. These trends at their highest present points are exemplified in reports such as those made by WEAVER (**9**), WEAVER and his associates (**8**), TURNER (**6**) and PEARSALL (**3, 4**), the latter having concluded that the relative sizes of plant organs conform to the equation $X = CY^k$, where X and Y are the sizes of the organs, C is a constant expressing their relative sizes, and indicates the ratio of their relative logarithmic growth rates and the spatial arrangements of their meristems. Obviously, this formula sets forth the relationship that the logarithm of stem weight is directly proportional to the logarithm of root weight. When the two time-series of logarithms are plotted against each other the result is a straight line.

In general, the available experimental evidence leads to the conclusion that herbaceous plants exhibit specific and varietal differences with respect to relative development of top and root under uniform environal conditions. However, few if any of the many types are non-plastic, that is, do not react to environmental changes by way of showing variations in the relative sizes of aerial and underground parts. The more intensive studies, particularly those made on growth rates, indicate that though variation occurs there is a persistent tendency towards positive correlation. The present writers have not examined growth rates but have obtained final weights on the tops and roots of lettuce, radish and tomato plants from a number of different experiments and have treated the data as shown later.

Methods of procedure

EXPERIMENTAL

In some of the experiments to be reported the plants were grown in greenhouse flats; in others in flower pots of different sizes. Whether grown in flats or pots the containers were set on boards to prevent the exit of the roots. Where pots were used, these were set on the bottom of the greenhouse bench and buried to their rims in moist sand. Any objection to the confinement of the roots in such containers can be met by the statement that this was simply one of the conditions under which top-root relations were measured. If the ultimate sizes of top and root are definitely and inevitably correlated, then the type of container might alter the degree of correlation but not destroy it nor change its character qualitatively. Furthermore, the use of flats and pots made it possible to recover the root systems readily and *in toto*. All the experiments were conducted in the greenhouse and every precaution taken to maintain uniform conditions of environment while any one of them was under way.

When the plants were grown in pots, the roots were obtained by freeing the whole mass from the pot, immersing it in a large volume of water, and gently kneading it with the hands until practically all of the soil was washed out. Following this, the root system was washed twice more in fresh water and then placed between layers of newspapers to dry off for a given length of time before the weight was taken.

When flats were used as containers, six plants were grown in each flat. The process for securing the separate root systems was that of dividing the mass of soil into six equal blocks; removing each one of the blocks by placing a square of galvanized iron under it, and immersing the block in water. From this point onward the method was the same as described previously for the plants grown in pots.

Mathematical

The top-root ratios were calculated in three ways: (1) as the quotient of mean (arithmetic) top to mean (arithmetic) root; (2) as the arithmetic mean of the individual top-root ratios, and (3) as the geometric mean of the individual ratios. The results from the use of these three methods of calculation on the same data differ sufficiently to necessitate making a choice among them. The properties of the geometric mean, when dealing with ratios, are such as to commend its use in preference to the others. On this mean and its probable error see Yule (**10**), Kelley (**2**), and Crist (**1**).

When the number of individuals in any lot of plants was less than 25, Pearson's (**5**) factors for the correction of the standard deviation were used and the corrected standard deviation substituted in all other calculations where the employment of the standard deviation was required.

The product-moment formula ($r = \frac{p}{\sigma_x \cdot \sigma_y}$) was used in calculating the coefficients of correlation. The probable error of r was obtained with the formula: $P.E._r = \frac{1 - r^2}{\sqrt{N}} \cdot 0.6745$.

No difference less than three times its probable error was considered significant, the probable error of the difference having been determined through the formula: $P.E._d = 0.6745\sqrt{\sigma_1^2 + \sigma_2^2}$.

Interpretation of the significance of the coefficient of correlation was made according to the following rules: (a) If r is 0.5 (plus or minus) or greater, correlation is practically certain. (b) In order to be reliable r must be at least four times its probable error. (c) If, under various conditions of experimentation, r persists in having the same sign, though not always significant in itself, there is some evidence of a general though weak relationship of the character of this sign between the two variables.

Experiments with lettuce (Grand Rapids Forcing variety)

Use of raw sulphur and superphosphate (c.p. and commercial.)—The seed was sown broadcast in greenhouse flats, the seedlings selected at the proper time, and transplanted to other flats (6 per flat) in which they were grown for a period of 51 days. The soil was a fertile fine sandy loam. The data appear in table I.

In each case shown in table I the ratio of the average top to average root R_1 is less than R (the arithmetic mean of the ratios for the plants individually), while Mg lies between these two. The probable error for any Mg is higher than for the corresponding R. This is the relationship between the three forms of average which holds as a general rule. Accordingly, only the geometric mean will be given and used hereafter in making comparisons.

The number of plants per lot was small, by design. This necessitated large differences, if they were to be significant. Under these conditions, superphosphate when applied either alone or along with raw sulphur, except in lot 4 where 800 pounds of the sulphur per acre were used, significantly increased the top-root ratio as compared with lots 1 and 2 where sulphur only was applied.

The ratios do not vary directly with the total weights of average plants. The smallest plants have the highest ratio, the largest plants have the second largest ratio, while the plants intermediate in size have the lowest ratios.

With so few plants none of the coefficients of correlation, including that for all the plants taken together, is significant. However, it is noteworthy that all of them are positive in character, one (lot 5) being above 0.5, and also that they do not vary consistently in magnitude with either the top-root ratios or with the average total weights of the plants.

Influence of calcium nitrate, potassium chloride and superphosphate.—The plants were grown in a very poor medium sandy loam soil in six inch pots. The nutrient treatments were applied in solution form at the beginning of the experiment. Further details and other data for this experiment may be found in Michigan Experiment Station Tech. Bull. 74. 1926. See table II for the results.

TABLE I

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR LETTUCE PLANTS

LOT	NUMBER OF PLANTS	SOIL TREATMENT	AVERAGE GREEN WEIGHT		R_1[a]	R[a]	Mg[a]	r[a]
			TOP	ROOT				
		lbs. per acre	*gm.*	*gm.*				
1	6	Sulphur, 400	86.8 ± 3.63	11.5 ± 0.31	7.52	7.56 ± 0.265	7.48 ± 0.270	0.433 ± 0.224
2	6	Sulphur, 800	89.3 ± 1.07	12.2 ± 1.07	7.33	7.54 ± 0.389	7.44 ± 0.401	0.169 ± 0.267
3	6	c.p. $CaH_4(PO_4)_2$, 1200	93.5 ± 3.43	10.0 ± 0.06	9.35	9.57 ± 0.470	9.46 ± 0.479	0.367 ± 0.238
4	6	c.p. $CaH_4(PO_4)_2$, 1200 plus sulphur, 800	90.6 ± 4.00	10.8 ± 0.02	8.39	8.38 ± 0.330	8.32 ± 0.337	0.333 ± 0.245
5	6	Commercial $CaH_4(PO_4)_2$, 1200	99.2 ± 2.52	9.3 ± 0.06	10.60	10.94 ± 0.550	10.80 ± 0.565	0.578 ± 0.186
6	6	Commercial $CaH_4(PO_4)_2$, 1200 plus sulphur, 400	84.0 ± 2.51	7.3 ± 0.07	11.50	12.53 ± 1.170	12.02 ± 1.255	0.296 ± 0.251
All	36							0.319 ± 0.100

[a] In all tables "R_1" is ratio of average top to average root; "R" average ratio of individual plants; "Mg" geometric mean of individual ratios; "r" coefficient of correlation.

TABLE II

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR LETTUCE PLANTS

LOT	NUMBER OF PLANTS	SOIL TREATMENT	AVERAGE GREEN WEIGHT			Mg	r
			TOP	ROOT	WHOLE PLANT		
		lbs. per acre	*gm.*	*gm.*	*gm.*		
1	14	Check	7.4 ± 0.27	7.9 ± 0.22	15.3	0.93 ± 0.029	0.481 ± 0.139
2	7	$Ca(NO_3)_2$, 100	14.6 ± 0.83	11.7 ± 0.74	26.3	1.25 ± 0.023	0.761 ± 0.107
3	7	$Ca(NO_3)_2$, 300	14.5 ± 0.84	9.1 ± 0.39	23.6	1.58 ± 0.102	0.276 ± 0.235
4	7	$Ca(NO_3)_2$, 600	20.4 ± 1.19	12.3 ± 0.53	32.7	1.64 ± 0.103	0.398 ± 0.214
5	7	$Ca(NO_3)_2$, 600 plus KCl, 300	22.9 ± 1.29	13.2 ± 0.25	36.1	1.71 ± 0.077	0.591 ± 0.166
6	7	$Ca(NO_3)_2$, 600 plus $CaH_4(PO_4)_2$, 300	35.0 ± 1.75	18.1 ± 1.06	53.1	1.95 ± 0.077	0.621 ± 0.156
7	7	$Ca(NO_3)_2$, 600 plus KCl, 300 plus $CaH_4(PO_4)_2$, 300	33.9 ± 2.16	16.6 ± 0.91	50.5	2.03 ± 0.166	0.243 ± 0.239
All	56						0.879 ± 0.020

Again, as in the preceding experiment, the number of plants per lot, except lot 1, was small. Nevertheless, table II shows that any nutrient treatment increased the top-root ratio and the ratios show an unmistakable tendency to be continuously higher as more complete fertilization of the soil obtains. The average weight of plant increases along with the ratios except in lots 3 and 7. In these cases the increased ratio does not indicate an absolute weight of top greater than in the preceding lot but is brought about by a reduction in the root which exceeds that in the top, thus leaving the top actually smaller, but still relatively larger than the root.

Though but one of the coefficients of correlation (lot 2) is significant, all are positive in sign; three of them (lots 2, 5, 6) being greater than 0.5. Here, as in the former experiment, these coefficients sustain no uniform relation to either the top-root ratios or the average total weights of the plants. When thrown together into one group, the 56 plants show strong positive correlation, the coefficient being 0.879 ± 0.020.

Use of acid and neutral soil with applications of hydrated lime and superphosphate.—Complete details of this experiment, which consisted primarily in a study of the acid tolerance of lettuce, can be found in Michigan State College Experiment Station Tech. Bull. 71. 1926, pages 14–18. The plants were grown in flats. Two types of soil were used. One soil was a mixture of two-thirds muck and one-third sand with a lime requirement of 20,000 pounds $Ca(OH)_2$ (Jones method). The second soil was a neutral fine sandy loam. The data, presented in table III, were taken when the plants had reached vegetative maturity. The number of plants per lot was larger than in either of the two former experiments.

The twenty-seven lots of plants listed in table III fall into five groups, namely, lots 1 to 6 with increasing amounts of lime; lots 7 to 10 with increasing applications of both lime and superphosphate; lots 12 to 17 with superphosphate constant while the lime treatments increase in size; lots 19 to 22 on neutral loam soil with superphosphate constant and lime applications increasing in size; lots 23 to 27 on neutral loam soil with increasing quantities of lime. Within any one of the five groups, the top-root ratios are approximately equal for the several lots, while at the same time, the average size of whole plants decreases with increased size of application of the materials used for soil treatment, due to both top and root being progressively smaller to about the same degree.

The effect of soil type is very pronounced. The top-root ratios on the acid muck-and-sand mixture are conspicuously higher than on the neutral sandy loam. This holds true where comparable treatments were used as well as for the checks. Relative root development in the acid muck-and-sand soil mixture was greatly reduced. This went to a very great extreme

TABLE III

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR LETTUCE PLANTS

LOT	NUMBER OF PLANTS	SOIL TREATMENT[c]	AVERAGE GREEN WEIGHT			Mg	r
			TOP	ROOT	WHOLE PLANT		
		tons per acre	*gm.*	*gm.*	*gm.*		
1[a]	24	Check	65.7 ± 2.24	8.8 ± 0.34	74.5	7.58 ± 0.254	0.540 ± 0.100
2	12	$Ca(OH)_2$, 2.5	70.3 ± 2.65	10.2 ± 0.47	80.5	6.94 ± 0.365	0.314 ± 0.176
3	12	$Ca(OH)_2$, 5.0	58.7 ± 1.93	9.7 ± 0.36	68.4	6.08 ± 0.368	−0.265 ± 0.181
4	12	$Ca(OH)_2$, 7.5	38.2 ± 1.45	6.0 ± 0.24	44.2	6.40 ± 0.237	0.408 ± 0.163
5	12	$Ca(OH)_2$, 10.0	26.0 ± 1.24	3.2 ± 0.19	29.2	8.32 ± 0.555	0.443 ± 0.156
6	12	$Ca(OH)_2$, 12.5	15.4 ± 0.94	1.8 ± 0.16	17.2	9.10 ± 0.742	0.678 ± 0.105
7	12	$Ca(OH)_2$, 3.4 plus $CaH_4(PO_4)_2$, 2	69.4 ± 3.03	5.4 ± 0.22	72.7	12.96 ± 1.821	0.358 ± 0.170
8	12	$Ca(OH)_2$, 6.8 plus $CaH_4(PO_4)_2$, 4	70.7 ± 2.03	6.4 ± 0.32	77.1	11.36 ± 0.567	0.447 ± 0.156
9	12	$Ca(OH)_2$, 10.0 plus $CaH_4(PO_4)_2$, 6	60.8 ± 1.94	4.9 ± 0.34	65.7	12.89 ± 1.008	0.287 ± 0.179
10	12	$Ca(OH)_2$, 13.4 plus $CaH_4(PO_4)_2$, 8	56.0 ± 2.11	4.3 ± 0.29	60.3	13.41 ± 0.613	0.618 ± 0.121
11	18	c.p. KH_2PO_4, 8	21.2 ± 1.71	3.2 ± 0.19	24.4	6.27 ± 0.414	0.664 ± 0.089
12	12	$CaH_4(PO_4)_2$, 8	24.7 ± 1.42	4.2 ± 0.28	28.9	5.95 ± 0.350	0.608 ± 0.123
13	12	$Ca(OH)_2$, 2.5 plus $CaH_4(PO_4)_2$, 8	81.8 ± 2.08	11.3 ± 0.46	93.1	7.33 ± 0.193	0.712 ± 0.096
14	12	$Ca(OH)_2$, 5.0 plus $CaH_4(PO_4)_2$, 8	75.3 ± 2.04	7.7 ± 0.31	83.0	9.94 ± 0.666	−0.460 ± 0.154
15	12	$Ca(OH)_2$, 7.5 plus $CaH_4(PO_4)_2$, 8	65.9 ± 1.30	10.6 ± 0.59	76.5	6.39 ± 0.309	0.522 ± 0.142
16	12	$Ca(OH)_2$, 10.0 plus $CaH_4(PO_4)_2$, 8	60.3 ± 2.23	8.8 ± 0.41	69.1	6.89 ± 0.361	0.356 ± 0.170
17	12	$Ca(OH)_2$, 12.5 plus $CaH_4(PO_4)_2$, 8	72.1 ± 2.58	11.1 ± 0.45	83.2	6.52 ± 0.411	−0.075 ± 0.194
18[b]	12	$CaH_4(PO_4)_2$, 2	16.9 ± 0.85	7.3 ± 0.36	24.2	2.30 ± 0.082	0.645 ± 0.114
19	12	$Ca(OH)_2$, 1 plus $CaH_4(PO_4)_2$, 2	18.1 ± 0.84	7.8 ± 0.27	25.9	2.28 ± 0.199	0.729 ± 0.091
20	12	$Ca(OH)_2$, 2 plus $CaH_4(PO_4)_2$, 2	21.5 ± 1.36	6.7 ± 0.25	28.2	3.15 ± 0.162	0.622 ± 0.119
21	12	$Ca(OH)_2$, 3 plus $CaH_4(PO_4)_2$, 2	17.9 ± 0.94	6.7 ± 0.36	24.6	2.65 ± 0.125	0.407 ± 0.163
22	12	$Ca(OH)_2$, 4 plus $CaH_4(PO_4)_2$, 2	14.0 ± 0.82	4.7 ± 0.35	18.7	3.12 ± 0.356	0.508 ± 0.144
23	12	Check	17.9 ± 0.83	8.0 ± 0.40	25.9	2.24 ± 0.090	0.605 ± 0.123
24	12	$Ca(OH)_2$, 1	18.7 ± 1.15	7.5 ± 0.28	26.2	2.42 ± 0.120	0.589 ± 0.127
25	12	$Ca(OH)_2$, 2	14.3 ± 0.93	5.6 ± 0.44	19.9	2.62 ± 0.121	0.748 ± 0.086
26	12	$Ca(OH)_2$, 3	9.6 ± 0.68	3.1 ± 0.11	12.7	2.99 ± 0.196	0.439 ± 0.157
27	12	$Ca(OH)_2$, 4	7.6 ± 0.48	2.6 ± 0.17	10.2	3.02 ± 0.098	0.797 ± 0.071
All	342						0.543 ± 0.026

[a] Lots 1 to 17 inclusive, soil was muck-and-sand mixture.

[b] Lots 18 to 27 inclusive, soil was neutral sandy loam.

[c] All nutrient substances of commercial grade, unless noted otherwise.

in lots 7 to 10 where the lime and the superphosphate were increased together.

In regard to the twenty-seven coefficients of correlation three, none of which is at all significant, are negative. Twenty-four of the coefficients, ten of which are above 0.5 and significant, are positive. Variation in the size of the coefficients is not consistent to any important extent with the soil treatments or the changes in the size of the plants and the ratios produced by these treatments. Correlation with all the plants taken in a single group is positive and clearly significant (0.543 ± 0.026).

INFLUENCE OF LENGTH OF DAY AS MODIFIED BY NUTRIENT TREATMENT.—The plants were grown singly, to vegetative maturity, in six-inch pots, the soil being a fine sand, low in fertility. Various nutrients were applied in different ways. The extra illumination of the plants designated as long-day plants was accomplished by means of 1000 watt Mazda lamps, socketed in porcelain enameled steel dome reflectors suspended at a height of 4.5 feet above the bench. Three of these bulbs, evenly spaced, were used over a bench 21 feet long and 5 feet wide, the pots containing the plants being distributed so as to give even illumination and also being systematically shifted about in their places once each week. The experiment was conducted during the short cloudy days of the winter season. The day for the long-day plants was lengthened 6 hours as an average. The plants of the short-day lots were covered each day at 3:00 P. M. and left covered until 9 o'clock the following morning. The covers consisted of specially built light-tight boxes each 10 feet long, 5 feet wide and 3 feet high, with light-tight ventilators arranged in each end. See table IV for the results.

An examination of table IV makes it clear that the top-root ratios were increased as the period of illumination was shortened. The differences for lots 1, 6 and 7, lots 2 and 8, and lots 3 and 9 are large and certainly significant. In the long-day group the nutrient treatments elevated the ratios decidedly. The increases in the short-day group are only apparent. Within groups, the increased ratios are associated with increased size of plant and greater actual weight of top, though the three largest ratios (lots 7, 8, 9) obtain with plants among the smallest in size. While the nitrate treatments of the short-day plants elevated the top-root ratios apparently, large plants were not produced as with the long-day treatments. Though raw materials from the soil have been sufficient, assimilable food products were not ample to give greater total growth more evenly distributed between top and root.

All of the coefficients of correlation are positive, three of them (lots 1, 6 and 9) giving evidence of certainty. The coefficient (0.685 ± 0.026) for all the plants, thrown together, is such as to make positive correlation certain.

TABLE IV

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR LETTUCE PLANTS

LOT	NUMBER OF PLANTS	DAY	SOIL TREATMENT	AVERAGE GREEN WEIGHT			Mg	r
				TOP	ROOT	WHOLE PLANT		
			gm. per pot	*gm.*	*gm.*	*gm.*		
1	21	Long	Check	11.2 ± 0.32	14.5 ± 0.65	25.7	0.79 ± 0.023	0.700 ± 0.075
2	21	"	$Ca(NO_3)_2$, 1	49.8 ± 1.58	18.9 ± 0.84	68.7	2.71 ± 0.177	0.355 ± 0.129
3	21	"	[a]$Ca(NO_3)_2$, 1	54.2 ± 2.28	11.3 ± 0.62	65.5	4.90 ± 0.373	0.363 ± 0.128
4	21	"	$Ca(NO_3)_2$, 1 plus $CaH_4(PO_4)_2$, 1	58.8 ± 1.58	15.1 ± 0.47	73.9	3.94 ± 0.171	0.133 ± 0.144
5	21	"	[a]$Ca(NO_3)_2$, 1 plus [a]$CaH_4(PO_4)_2$, 1	75.2 ± 1.77	16.7 ± 0.84	91.9	4.72 ± 0.320	0.385 ± 0.125
6	15	Normal	Check	11.0 ± 0.62	4.5 ± 0.47	15.5	2.84 ± 0.590	0.713 ± 0.086
7	20	Short	Check	8.5 ± 0.32	1.4 ± 0.13	9.9	6.88 ± 1.101	0.417 ± 0.125
8	22	"	$Ca(NO_3)_2$, 1	15.1 ± 0.52	1.5 ± 0.11	16.6	10.84 ± 1.000	0.352 ± 0.126
9	22	"	[a]$Ca(NO_3)_2$, 1	13.4 ± 0.59	1.7 ± 0.14	15.1	8.74 ± 0.701	0.582 ± 0.095
All	184							0.685 ± 0.026

[a] Applied cumulatively in fourth portions.

INFLUENCE OF LENGTH OF DAY IN CONJUNCTION WITH NUTRIENT TREATMENTS (SECOND EXPERIMENT).—This experiment differed from the preceding one in that it was performed during the spring season (April 17 to May 23), the former having been conducted in midwinter. The short-day plants had a day of eight hours, the long-day plants 16 to 18 hours, while the normal day was approximately 10 to 12 hours in length. Otherwise, the two experiments were duplicated as to methods. The results are shown in table V.

The data in table V confirm the main conclusion that was evident from the results of the preceding experiment, namely, that the top-root ratio was raised as the day was shortened, either with or without the nitrate treatments. In two of the three groups the nitrate of itself significantly increased the ratio. Again, the highest ratios are for the short-day plants and are associated with the smallest plants which, at the same time, have the lowest actual weight of top, as well as root.

All of the coefficients of correlation are positive, three of them being about 0.5 and no one of these three less than five times its probable error. The coefficient for the 178 plants is positive, more than 0.5, and is 21 times its probable error.

EXPERIMENTS WITH RADISH PLANTS (SCARLET GLOBE VARIETY)

USE OF NUTRIENT SUBSTANCES ON TWO SOILS OF DIFFERENT COMPOSITION.—One of the two soils, the one designated as A in table VI was composed of five parts fine sandy loam and one part medium coarse sand; the other, B, of these types of soil, with the proportions reversed. These soils were treated as shown in table VI, and used in six-inch pots in which the plants were grown singly.

Table VI shows that the nutrient treatments increased the average size of plant on each one of the two soils but the top-root ratio was not changed significantly. With one exception (lot 6) the average plant was larger on soil B than soil A, while at the same time the ratio of top to root is consistently lower, though the differences are not strictly real except as between lots 1 and 2.

The ten coefficients of correlation are positive; seven of them being above 0.5. Of these seven, three are fully significant. The coefficient (0.694 ± 0.031) for all the plants indicates certain positive correlation.

EFFECT OF LENGTH OF DAY AS MODIFIED BY NUTRIENT TREATMENTS

This experiment was made simultaneously with the one on lettuce, the data for which are contained in table IV, using the same general methods of procedure. The period of illumination for the long-day plants was six

TABLE V

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR LETTUCE PLANTS

LOT	NUMBER OF PLANTS	DAY	SOIL TREATMENT	AVERAGE GREEN WEIGHT			Mg	r
				TOP	ROOT	WHOLE PLANT		
			gm. per pot	*gm.*	*gm.*	*gm.*		
1	30	Long	Check	54.5 ± 1.43	34.3 ± 0.74	88.8	1.58 ± 0.033	0.625 ± 0.076
2	30	"	$NaNO_3$, 1	79.4 ± 0.85	39.4 ± 0.72	118.8	2.03 ± 0.031	0.543 ± 0.086
3	29	Normal	Check	55.4 ± 1.21	26.3 ± 0.62	81.7	2.11 ± 0.055	0.324 ± 0.111
4	30	"	$NaNO_3$, 1	83.0 ± 1.13	39.8 ± 0.99	122.8	2.12 ± 0.053	0.340 ± 0.109
5	29	Short	Check	46.9 ± 0.88	17.8 ± 0.51	64.7	2.67 ± 0.064	0.491 ± 0.095
6	30	"	$NaNO_3$, 1	68.2 ± 1.19	17.3 ± 0.46	85.5	3.98 ± 0.108	0.295 ± 0.113
All	178							0.573 ± 0.027

TABLE VI

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR RADISH PLANTS

Lot	Number of plants	Soil	Soil treatment	Average green weight			Mg	r
				Top	Root	Whole plant		
			gm. per pot	*gm.*	*gm.*	*gm.*		
1	12	A	Check	3.3 ± 0.20	6.2 ± 0.19	9.5	0.51 ± 0.026	0.763 ± 0.082
2	15	B	Check	3.2 ± 0.16	7.8 ± 0.42	11.0	0.41 ± 0.017	0.584 ± 0.115
3	12	A	$Ca(NO_2)_3$, 1	3.5 ± 0.19	7.0 ± 0.43	10.5	0.49 ± 0.057	0.356 ± 0.170
4	15	B	$Ca(NO_3)_2$, 1	5.6 ± 0.33	14.3 ± 0.78	19.9	0.39 ± 0.020	0.621 ± 0.107
5	12	A	KCl, 1	3.6 ± 0.26	7.7 ± 0.38	11.3	0.45 ± 0.034	0.590 ± 0.127
6	15	B	KCl, 1	2.9 ± 0.13	8.0 ± 0.38	10.9	0.36 ± 0.020	0.566 ± 0.119
7	12	A	$Ca(NO_3)_2$, 1 plus KCl, 1	3.9 ± 0.34	7.4 ± 0.28	11.3	0.50 ± 0.046	0.265 ± 0.181
8	15	B	$Ca(NO_3)_2$, 1 plus KCl, 1	3.6 ± 0.17	9.5 ± 0.36	13.1	0.38 ± 0.019	0.533 ± 0.125
9	6	A	$CaH_4(PO_4)_2$, 1	4.2 ± 0.24	8.0 ± 0.66	12.2	0.53 ± 0.029	0.586 ± 0.181
10	15	B	$CaH_4(PO_4)_2$, 1	4.2 ± 0.25	9.1 ± 0.54	13.3	0.47 ± 0.061	0.387 ± 0.148
All	129							0.694 ± 0.031

TABLE VII

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR RADISH PLANTS

LOT	NUMBER OF PLANTS	DAY	SOIL TREATMENT	AVERAGE GREEN WEIGHT			Mg	r
				TOP	ROOT	WHOLE PLANT		
			gm. per pot	*gm.*	*gm.*	*gm.*		
1	22	Long	Check	3.5 ± 0.09	7.0 ± 0.26	10.5	0.51 ± 0.023	0.261 ± 0.134
2	21	"	$Ca(NO_3)_2$, 1	7.6 ± 0.46	11.8 ± 0.51	19.4	0.62 ± 0.031	0.637 ± 0.088
3	22	"	KCl, 1	3.5 ± 0.13	6.1 ± 0.39	9.6	0.61 ± 0.044	0.487 ± 0.110
4	22	"	$Ca(NO_3)_2$, 1 plus KCl, 1	8.6 ± 0.43	12.3 ± 0.53	20.9	0.70 ± 0.059	0.212 ± 0.138
5	15	Normal	Check	2.1 ± 0.03	3.2 ± 0.19	5.3	0.67 ± 0.059	0.131 ± 0.171
6	16	Short	Check	1.6 ± 0.09	1.1 ± 0.14	2.7	1.74 ± 0.216	0.511 ± 0.125
7	16	"	$Ca(NO_3)_2$, 1	2.2 ± 0.19	1.1 ± 0.11	3.3	2.10 ± 0.486	0.444 ± 0.136
8	14	"	KCl, 1	1.6 ± 0.11	1.2 ± 0.12	2.8	1.62 ± 0.249	0.558 ± 0.124
All	148							0.824 ± 0.018

hours in excess of the normal day, while that for the short-day plants was four to five hours less than normal. The soil was a medium coarse sand, low in fertility. Table VII gives the results.

With these plants (table VII), as with the lettuce plants (table IV), the top-root ratio increased as the day was shortened, the difference between lot 1 and lot 6 being highly significant. The increases in the ratio are accompanied by decreases in plant size, development in lots 6, 7 and 8 being very meager. Increases in the ratio due to nutrient treatments are only apparent. As to size of plant, the nitrate was effective, more effective with the long than short day.

Each of the eight coefficients of correlation is positive in character. Among the three that exceed 0.5, lot 2 is significant. The coefficient for the plants as a whole (0.824 ± 0.018) is especially high and reliable.

Experiments with tomato plants

Effect of size of container on top-root relation.—Pure line seed of the John Baer variety was sown on July 28. On August 14, the seedlings were potted singly in three-inch pots and remained in these until September 7. On the latter date, 51 of the plants were selected at random and weights of their tops and roots secured. Forty-one plants were shifted to five-inch pots, 41 to eight-inch pots, and 41 to 10-inch pots on September 9. The soil, a fine sandy loam, high in organic matter, was the same for each of the four lots. No manuring of any kind was done. The experiment was concluded on October 10, when the plants in the five-inch pots were just beginning to show symptoms of deterioration because of becoming potbound. The leaves and stem were weighed separately. See table VIII for the results.

The data in table VIII make it practically certain that the ratio of top to root rose as larger pots were used. This holds true whether the calculations are based on whole top, on stem, or on leaves. The plants grew to greater size in the larger containers, with both stem and leaves increasing in weight and each of these making greater relative growth than the root. The leaves constitute a greater percentage of the entire top than the stem, and gain in this respect occurs while the stem loses as the pots are larger. Furthermore, the gain in size relative to the roots is greater for the leaves than it is for the stem. The ratio of top to root for lot 2 as compared with lot 1 is not significantly different, while with lots 3 and 4 the ratios are clearly higher.

All of the coefficients of correlation are positive and all fully significant. Six of the nine are above 0.5. Though the differences are not always equal to three times their probable errors, the indication that the degree of corre-

TABLE VIII

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR TOMATO PLANTS

LOT	NUMBER OF PLANTS	SIZE OF POT	AVERAGE GREEN WEIGHT				Mg	r
			AERIAL PART*		ROOT	TOTAL		
		inches		*gm.*	*gm.*	*gm.*		
1	51	3	Top	4.7 ± 0.24	1.8 ± 0.09	6.5	2.19 ± 0.055	0.899 ± 0.018
2	41	5	Top	25.3 ± 1.27	12.5 ± 0.34	37.8	1.94 ± 0.060	0.718 ± 0.051
			Stem	10.6 ± 0.40	12.5 ± 0.34	23.1	0.84 ± 0.016	0.793 ± 0.039
			Leaves	14.7 ± 0.90	12.5 ± 0.34	27.2	1.10 ± 0.049	0.663 ± 0.059
3	41	8	Top	57.0 ± 1.47	19.1 ± 0.35	76.1	2.96 ± 0.074	0.471 ± 0.081
			Stem	22.7 ± 0.57	19.1 ± 0.35	41.8	1.18 ± 0.028	0.504 ± 0.078
			Leaves	34.2 ± 0.94	19.1 ± 0.35	53.4	1.78 ± 0.043	0.462 ± 0.083
4	41	10	Top	82.9 ± 0.77	26.3 ± 0.36	109.2	3.17 ± 0.043	0.457 ± 0.083
			Stem	30.2 ± 0.35	26.3 ± 0.36	56.5	1.15 ± 0.049	0.509 ± 0.078
			Leaves	52.7 ± 0.55	26.3 ± 0.36	79.0	2.01 ± 0.032	0.345 ± 0.092
All	174	All	Top					0.948 ± 0.005
All	123	All	Stem					0.890 ± 0.013
All	123	All	Leaves					0.881 ± 0.013

* Part of plant set in ratio to and correlated with root.

lation lessened as the containers were larger and that the correlation between root and stem was the most pronounced, is quite certain. This means that the degree of correlation lessened as the plants became larger and the ratios of aerial to underground parts increased. Correlation of top and root for the entire number of plants (174) is nearly perfect, while tending to be slightly less for stem and root, and for leaves and root.

INFLUENCE OF DEFLOWERING ON PRUNED AND UNPRUNED PLANTS.—In this experiment, the plants were of the Grand Rapids Forcing variety and were brought along to the stage for transplantation to pots in the same manner as those of the preceding experiment. They were transplanted to six-inch pots and grown therein on a fine sandy loam soil, well supplied with organic matter, for a period of 33 days. One lot of 84 plants was kept trained to a single stem, another lot of the same number allowed to go unpruned. Forty-two plants of each of these two groups had the flowers of the clusters (3 clusters mostly) removed as they opened. See table IX for the data.

Table IX shows some differences which appear consistent, though none of them is great enough to be considered significant. The plants are larger and the ratios higher for the unpruned plants than for the pruned and in both of these two groups larger plants with higher ratios obtain for those from which the flowers were not removed. Thus, higher ratios are apparently associated with the heavier plants.

With the eighteen coefficients of correlation, thirteen are greater than 0.5, and no one of the eighteen is rendered unreliable by the size of its probable error. Though the differences in the coefficients are consistent, being higher for the unpruned than the pruned, and higher for the plants from which the flowers were removed, they are too small, without exception, to be significant.

EFFECT OF BOTTOM HEAT ON PRUNED AND UNPRUNED PLANTS.—The work here differed from that for which the results have been given in table IX only in that bottom heat was supplied to the bench wherein the pots were placed. This elevated the temperature of the plants as a whole but especially that of the soil and the roots it contained. The arrangement for bottom heat was that of steam pipes swung under the bench at a distance of about 18 inches from the bottom of the bench, and heavy burlap, reaching to the floor, hung around the sides of the bench. Heat was kept on during the nights, sufficiently to hold the temperature of the moist sand about the pots at a point averaging about 15 degrees above that of another bench not provided with bottom heat. The results are presented in table X.

In table X, the top-root ratios are higher for the unpruned than the pruned plants, though the differences are small and insignificant. Comparing the data with those from table IX for corresponding groups of plants

TABLE IX

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR TOMATO PLANTS

LOT	NUMBER OF PLANTS	GROUP	FLOWERS	AVERAGE GREEN WEIGHT				Mg.	r
				AERIAL PART*		ROOT	TOTAL		
					gm.	gm.	gm.		
1	42	Pruned	Off	Top	27.4 ± 0.78	9.2 ± 0.17	36.6	2.92 ± 0.067	0.573 ± 0.070
				Stem	12.8 ± 0.29	9.2 ± 0.17	22.0	1.36 ± 0.025	0.644 ± 0.061
				Leaves	14.7 ± 0.52	9.2 ± 0.17	23.9	1.54 ± 0.047	0.501 ± 0.078
2	42	Pruned	On	Top	31.2 ± 1.02	10.1 ± 0.21	41.3	3.01 ± 0.105	0.510 ± 0.077
				Stem	14.0 ± 0.38	10.1 ± 0.21	24.1	1.37 ± 0.038	0.565 ± 0.070
				Leaves	17.2 ± 0.67	10.1 ± 0.21	27.3	1.63 ± 0.070	0.460 ± 0.082
All	84			Top					0.405 ± 0.061
				Stem					0.444 ± 0.059
				Leaves					0.362 ± 0.064
3	42	Unpruned	Off	Top	33.7 ± 1.09	10.4 ± 0.22	44.1	3.17 ± 0.081	0.668 ± 0.057
				Stem	15.9 ± 0.46	10.4 ± 0.22	26.3	1.51 ± 0.032	0.696 ± 0.054
				Leaves	17.8 ± 0.65	10.4 ± 0.22	28.2	1.64 ± 0.050	0.626 ± 0.060
4	42	Unpruned	On	Top	34.7 ± 1.19	9.8 ± 0.20	44.5	3.44 ± 0.114	0.520 ± 0.076
				Stem	16.3 ± 0.48	9.8 ± 0.20	26.1	1.63 ± 0.046	0.549 ± 0.073
				Leaves	18.5 ± 0.73	9.8 ± 0.20	28.3	1.80 ± 0.077	0.463 ± 0.082
All	84			Top					0.577 ± 0.049
				Stem					0.607 ± 0.047
				Leaves					0.526 ± 0.053

* Part of plant set in ratio to and correlated with root.

TABLE X

TOP-ROOT RATIOS AND COEFFICIENTS OF CORRELATION FOR TOMATO PLANTS

LOT	NUMBER OF PLANTS	TREATMENT (BOTTOM HEAT)	AVERAGE GREEN WEIGHT				Mg	r
			AERIAL PART*		ROOT	TOTAL		
				gm.	gm.	gm.		
1	47	Unpruned	Top	44.7 ± 0.98	11.8 ± 0.16	56.5	3.70 ± 0.059	0.717 ± 0.069
			Stem	18.2 ± 0.37	11.8 ± 0.16	30.0	1.52 ± 0.021	0.748 ± 0.043
			Leaves	26.5 ± 0.64	11.8 ± 0.16	38.3	2.18 ± 0.042	0.687 ± 0.052
2	51	Pruned	Top	47.7 ± 1.18	13.1 ± 0.20	60.8	3.57 ± 0.067	0.675 ± 0.051
			Stem	19.0 ± 0.39	13.1 ± 0.20	32.1	1.44 ± 0.025	0.614 ± 0.059
			Leaves	28.7 ± 0.82	13.1 ± 0.20	41.8	2.12 ± 0.047	0.675 ± 0.051
All	98	Top						0.690 ± 0.036
		Stem						0.661 ± 0.038
		Leaves						0.671 ± 0.038

* Part of plant set in ratio to and correlated with root.

(lots 2 and 4) it becomes apparent that the use of bottom heat greatly increased the size of average plants. It also led to higher top-root ratios, the difference for the pruned plants being significant.

Each of the nine coefficients of correlation is positive, above 0.5 and fully reliable. None of the apparent differences between the coefficients that are comparable are significant. Better correlation of aerial parts with root obtained than in the preceding experiment, but the differences are only apparent.

Discussion and conclusions

Under any given circumstances an herbaceous plant has a definite possibility as regards total growth and ultimate size. But, while the plant is a unit, functioning and developing as an organic whole, there are distinctions of degree as regards the top and root. Significant variations in the relative distribution of growth between top and root occur naturally and may be readily induced by experimentation. The two parts are dependent, and, in general, they increase together, but not in a continuous and fixed proportion, whatever the time in the life cycle and the environment may happen to be. This is fully substantiated by comparisons of top-root ratios, even when the data are subjected to the standard tests of statistical analysis and the geometric type of average used in the process of interpretation. PEARSALL (**4**) points out that the value of k (ratio of average logarithmic growth rates) in the equation $S = cR^k$ varies with conditions of growth, as well as the type of plant. With etiolated seedlings of *Pisum sativum,* k was 2 to 3 times as great as when the plants were grown in the light. High nitrogen also elevated the value of k.

Though the relative development of top and root varies widely in nature and under experimental conditions, the two parts show a persistent interdependence on the basis of their respective final masses. While this relationship is neither markedly close nor constant in degree, it is present, in general, as a permanent characteristic. Top and root in higher plants, except in a few forms like certain species of *Tillandsia* which are rootless, other organs discharging the functions of roots, vary concomitantly. Generally speaking, correlation between top and root is positive, or in other words, increased size of top is accompanied by increased size of root or *vice versa.* This principle is deducible from the correlation coefficients that have been presented, though not as certainly from the top-root ratios. The ratios are somewhat inadequate, based as they are on the absolute values of weight. The coefficients of correlation which are derived through deviations from the line of average relationship afford the necessary criteria.

An examination of the preceding tables shows little or no tendency of the size of the plant to be dependent upon or governed by the degree of correlation between root and top with respect to final mass. Correlation is certainly positive in character, but it does not show itself to be stronger as the plants average larger in total weight, nor less as they average smaller. In fact, if there be any relationship at all of this kind, it tends to be negative rather than positive. More often, the higher coefficients of correlation are associated with average plants that are relatively smaller. From this it may be inferred that when conditions are such as to leave the growth of the whole plant less restricted, correlation between top and root appears to be lessened.

These facts help to explain the wide range of plant adaptation observed in nature. In so far as survival, establishment and perpetuation hinge upon changes in relative development of top and root to meet existing conditions, the margin of possibility is quite great. Likewise, the position of the practical grower is rendered advantageous. He has considerable latitude by way of opportunity to alter relative size of top and root in seeking to realize his desires. An "ideal balance" from the gardener's standpoint is one which promotes the plant's thrifty development, while at the same time its growth respecting time, amount, type and place (localization in plant part) is such as to suit his material purpose. When the fact of the plant's plasticity is known, it remains essential that the proper means for producing desirable modifications be understood; and furthermore, that the limits of variability, which if exceeded will endanger the plant as a whole, be respected.

Summary

LETTUCE EXPERIMENTS.—1. The top-root ratio varied with experimental conditions between the extremes of 0.79 (table IV, lot 1) and 12.96 (table III, lot 7).

2. Under the following circumstances the top-root ratio was increased: Application of superphosphate either alone or with raw sulphur on a fertile fine sandy loam soil (table I); progressive improvement of fertility in a very poor medium sandy loam soil (table II); with an acid muck-and-sand soil mixture as compared with a fertile fine sandy loam, neutral in reaction (table III); the addition of both lime and superphosphate to an acid muck-and-sand soil mixture (table III); shortened period of daylight illumination in comparison with either normal or artificially lengthened day (tables IV and V); use of sodium nitrate alone and with superphosphate in conjunction with either long or short-day light treatment (tables IV and V).

3. The top-root ratio was lowered by long-day illumination (tables IV and V).

4. The coefficients of correlation for the separate lots of plants vary widely and show no definite relation, respecting their magnitude, to average

sizes of whole plants, but on the whole are decidedly positive in character. The coefficient of correlation for all lettuce plants taken together as a single group (975 individuals) is 0.521 ± 0.018.

RADISH EXPERIMENTS.—5. The top-root ratio was higher for plants grown on a soil composed of 5 parts fine sandy loam and 1 part medium coarse sand than for those on soil of same components but with the proportion reversed (table VI).

6. As with lettuce, the top-root ratio was higher for short-day plants and lower for long-day plants in comparison with normal-day plants (table VII).

7. Correlation between top and root was variable in degree but clearly positive in character. The coefficient for all radish plants grouped together (277 individuals) is 0.728 ± 0.019.

TOMATO EXPERIMENTS.—8. The ratios, whether based on the mass relation of whole top, leaves only, or stem only to the root, increased as the size of the container used was greater (table VIII).

9. Higher ratios obtained consistently (though the differences are not mathematically certain) for unpruned plants, for non-deflorated plants both pruned and unpruned, and for plants provided with bottom heat (tables IX, X).

While none of the differences between the coefficients of correlation for the several experimental lots is great enough to be mathematically significant, it is noteworthy that the coefficients are apparently higher for unpruned than pruned plants, for plants from which flowers were removed than those not treated so, for plants grown in larger containers, and also higher as between root and stem than between root and either whole top or only the leaves. The coefficients are more consistent than for either the lettuce or radish plants and the positive nature of correlation even more evident. The coefficient of correlation with all tomato plants thrown into one group is for whole top and root (440 individuals) 0.885 ± 0.007; stem and root (389 individuals) 0.792 ± 0.013; leaves and root (389 individuals) 0.836 ± 0.010.

GENERAL.—The concrete results that have been presented are not altogether new and different. In the main, they confirm other investigations in showing the great variability possible in the mass relation of top to root, and give credence to the idea of an "ideal balance" obtainable, within limits, by nature in the process of natural plant adaptation and by plant growers to suit their needs and purposes. It is thought, however, that improved methods for the analysis of data of this type, especially use of the geometric mean and the coefficient of correlation, have been employed, and furthermore, that the fact of persistent positive correlation in size of top and root, regardless of the wide variation shown under special conditions, has been demonstrated.

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